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## Research

### Urbanization shapes the relation between density and melanin-based colouration in bird communities

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Growing urbanization increasingly influences ecosystems worldwide. While the effects of urban conditions within species (through either plastic or evolutionary responses) have been widely studied, their potential influences among species (through environmental filter), especially concerning their colouration, remain poorly known. Here, we investigated whether avian communities breeding inside and outside a major European city (Paris) differ with regards to melanin-based plumage colouration. Melanins are heritable pigments present in many taxa and have a series of unique properties that may allow coping with urban conditions. Using melanin-based colouration as an integrative phenotypic marker, we predicted 1) that the probability of breeding inside the city should increase with the intensity of species melanin-based colouration, 2) that for species breeding both inside and outside the city, density should increase with the intensity of dark colouration inside the city, but not outside the city and 3) that species not breeding inside the city should not exhibit this positive relation between density and colouration. Our results confirmed these predictions. In addition, the density of species not breeding inside the city decreased with the darkness of their plumage. Altogether, these results suggest that bird species experience a balance between costs and benefits of melanin-based colouration shaped by environmental conditions. Both the environmental filtering and the urbanisation-shaped relation between density and colouration evidenced here are likely a general trend, however possibly modulated by additional local environmental conditions. Their importance may even be underestimated given the restricted geographical scale and the overall urbanization rate of the region studied. Further studies involving regions with contrasted environmental conditions should gain insight into the consequences of urbanization worldwide on traits associated with melanin-based colouration.

Keywords: birds, colouration, communities, environmental filter, melanin, urbanization



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## Introduction

Human activities exert a major influence on biodiversity functioning and evolution (Caro et al. 2012), and ecosystems considered as 'ecologically intact' currently represent a surface lower than 3% worldwide (Plumpton et al. 2021). Original environments have been mainly replaced by cultivated landscapes and cities. Urbanization has profound ecological and evolutionary consequences due to a series of novel environmental conditions (habitat fragmentation, noise, light, chemical, electromagnetic pollutions, food abundance, traffic, human presence, altered ecosystem functioning and biotic interactions; Breuste et al. 2013, Szulkin et al. 2020). There is growing evidence that these conditions exert both environmental filters at the communities level and selective pressures within member species.

Among terrestrial vertebrates, birds have the highest proportion of species reported in cities (Aronson et al. 2014, Ducatez et al. 2018). Urbanization leads to a reduction in bird species richness, their ecological functions and their evolutionary uniqueness, and to an increase in their local abundance (Morelli et al. 2016, Batáry et al. 2018, Evans et al. 2018, La Sorte et al. 2018, Leveau 2019). At the intraspecific level, urbanization acts as a selective pressure, leading to phenotypic differentiations between urban versus non-urban populations within species (reviewed by Alberti 2015, Isaksson 2018, Szulkin et al. 2020). At the interspecific level, evidence exists that urbanization acts as an environmental and phylogenetic filter: bird species in the cities do not represent a random sample from the overall region, but instead exhibit particular characteristics (Bonier et al. 2007, Evans et al. 2011, Sol et al. 2014, Marzluff 2017, Ducatez et al. 2018, Leveau 2019).

Melanins are the most common pigments in animals and plants and are mostly responsible for dark colouration. They are notoriously known to be associated with UV protection, thermoregulation and camouflage (Hill and McGraw 2006), but they have a much longer list of properties (d'Ischia et al. 2015, McNamara et al. 2021). Among these, some may help coping with environmental conditions in cities, being beneficial either to melanic individuals within urban species (intraspecific level) or to species within urban communities (interspecific level). First, melanins confer a higher physical resistance to tissue abrasion (e.g. feathers, Bonser et al. 1995), likely beneficial in cities where abrasive surfaces are widespread. Second, the higher resistance to parasites associated with melanins (McGraw et al. 2000, Côte et al. 2018) may be advantageous in cities where the prevalence of some parasites may be elevated (Giraudeau et al. 2014). Third, the higher resistance to stress melanins provide (Almasi et al. 2010) may be favorable in urban areas characterized by multiple stressors such as increased temperature (known as the 'heat-island effect') or anthropogenic disturbances in the cities. Fourth, melanins have metal-binding properties (Riley 1997) which may improve detoxication of toxic metals through their sequestration in inert body parts such as feathers away from the bloodstream (Chatelain et al. 2014,

2016), which would be advantageous in cities where levels of toxic metals are elevated. Fifth, their pleiotropic associations with higher levels of aggressiveness (Ducrest et al. 2008) may be beneficial in cities where populations reach higher densities. Each of these five properties associated with melanins may thus separately increase the ability to cope with urban conditions, and the overall sum of their effects all point to a global advantage of exhibiting elevated melanin productions in cities. Consequently, a covariation between melanin-based colouration and levels of urbanization is expected, both at intraspecific and interspecific levels. Accordingly, at the intraspecific level, polymorphic species (insects, birds and reptiles) tend to be more melanic in urban areas, possibly due to camouflage, parasitism reduction and detoxification (Obukhova 2007, Jacquin et al. 2013; reviewed by Leveau 2021). At the interspecific level however, studies on the covariation between melanin-based colouration and urbanization are scarce, requiring investigations on how urbanization filters species according to their colours (Leveau 2019, 2021).

Here, we investigated whether the intensity of plumage darkness, used as a proxy of melanic colouration and as an integrative phenotypic marker linked with many other traits, is associated with city-dwelling in bird communities. We tested for a potential relation between the intensity of melanin-based colouration and both the probability of breeding and the density of bird species inside a highly urbanized European city (Paris), as well as the density in the surrounding region (Île-de-France). Based on our hypothesis that melanin-based colouration would be advantageous in urban areas, we specifically predicted 1) that the probability for bird species to breed inside the city should increase with their melanin-based colouration, 2) that density of species breeding inside (and outside) the city should increase with their melanin-based colouration in the city, while 3) density outside the city of species not breeding in the city should not exhibit this association with melanin-based colouration.

## Material and methods

### Geographical zone: region Île-de-France and Paris city

The administrative city of Paris (intramuros, excluding both woods Vincennes and Boulogne) is located approximately near the middle of the region Île-de-France. It represents a surface of 0.88% of the region (87 km<sup>2</sup> out of 12 012 km<sup>2</sup>; see Supporting information, summarizing main characteristics of interest for both region and city). We calculated a proxy of urbanization rates, both inside and outside the city, by summing the percentages of impervious surface represented by quarries, landfills, building sites, equipments, water, individual housing, collective housing, activities, transports open artificialized spaces (data from <www.institutparisregion.fr/>, year 2017; Supporting information). Importantly, urbanization rates within Paris (80 km<sup>2</sup>/87 km<sup>2</sup> = 92.50%) and outside Paris (2802 km<sup>2</sup>/12 012 km<sup>2</sup> = 24.00%) greatly differ ( $\chi^2_1 = 218.22$ ,  $p < 2.2 \times 10^{-16}$ ).

## Breeding status, abundance and density of bird species in city and in region

Data were extracted from a regional bird atlas (Le Maréchal et al. 2013) based on data from Malher et al. (2010). According to this atlas, 355 species were observed at least once in the Ile-de-France region, among which 151 bird species (in 103 genera in 49 families in 18 orders) were documented as breeding in the whole Île-de-France region. For each of these 151 bird species, we extracted breeding status inside Paris (breeding versus non-breeding), minimum and maximum abundance estimations, and we calculated mean abundance and mean density (as the mean between minimum and maximum abundance estimations, divided by surface) inside and outside Paris (i.e. in the rest of the region Île-de-France, where abundance and surface were calculated as the ones in the region minus the ones in the city). On average, mean abundance was  $37\,145 \pm \text{SD } 137\,041$  individuals per species.

## Bird traits

We extracted body size, longevity and feeding regime (granivorous, herbivorous, insectivorous, omnivorous, piscivorous, vegetarian, carnivorous) for each species. Longevity was finally not used to avoid colinearity issues due to its significant association with body size ( $\chi^2_1 = 33.54$ ,  $p = 7 \times 10^{-09}$ ) and because it may strongly depend on environmental conditions linked with urbanization, making it likely unreliable. Body size and feeding regime were not statistically associated ( $\chi^2_3 = 3.31$ ,  $p = 0.65$ ) and were therefore included in the models.

## Scoring bird species melanin-based colouration

We attributed a score of melanin colouration to every species documented in the region. To reach objectivity and reliability of colouration proxies, we used three independent approaches, one of each respectively realized by one of three co-authors initially blind to the hypothesis: 1) a binary score (attributed by AM) distinguished between melanin-poor species (for which dark colour represents less than 50% of total male body surface) and melanin-rich species (for which dark colour represents more than 50% of total male body surface), based on pictures and drawings from Hume et al. (2011); 2) a first continuous score (determined by MG) calculated as the sum of scores (from 0 white, 1 light grey, 2 striped or spotted light grey, 3 dark grey, 4 black-striped or black-spotted dark grey, to 5 totally black) attributed to each of 12 bodyparts (throat, chest, belly, flank, undertail, underwings, head, mantle, upperwings, rump, uppertail coverts, tail) based on bird photographs (<[www.oiseaux.net](http://www.oiseaux.net)>), averaged between males and females; 3) a second continuous score (calculated by NT), calculated following Biard et al. (2009, adapted from Yezzerinac and Weatherhead 1995) as the sum of melanic colouration scores (from 0 white, to 4 black, based on drawings from a field guide (Svensson et al. 2014) to limit

the influences of light conditions on colour perception) attributed to each of 7 body parts weighted by the percentage of the body surface it typically represents (chin, cheeks and above eye 8%; breast 23%; belly 10%; crown and nape 11%; back 15%; wings 20%; tail 6%; bill, legs and feet were excluded to focus on plumage colour), averaged between males and females.

The repeatability of the latter scoring method has been previously found to be very high ( $R > 0.87$ ; Biard et al. 2009), but the repeatability of the binary scoring method used here has never been tested for. To evaluate the repeatability of our scoring methods, 4 additional observers independently attributed a score on a subset of 21 species.

## Statistical analyses

We first estimated the repeatability of our scoring methods. Then, using the three scores independently attributed, a consensus proxy of melanin score was then calculated for each bird species by extracting the coordinates on the first axis of a principal components analysis realized on all three scores (hereafter called 'axis 1 of PCA').

We also checked the reliability of scoring methods by testing for their correlation through generalized linear models, with either binomial (for binary score melanin-rich versus melanin-poor) or normal distribution (for continuous scores).

We compared the distributions of melanin-based colouration (axis 1 of PCA) between species breeding inside Paris and species which do not, with Kolmogorov–Smirnov tests.

In all further models, Genus was nested within Family nested within Order as random effect, to take phylogeny into account (i.e. non-independency between closely related species which may otherwise result in pseudo-replication on trait values and on the propensity to breed and thrive in urban areas). Due to overdispersion (i.e. deviance/residual degrees of freedom larger than 1), we specified quasibinomial (for breeding status) or quasipoisson (for densities) distributions.

We tested for a relation between breeding status inside Paris and colouration by fitting a generalized linear mixed-effects model with breeding status inside Paris as binary dependent variable, colouration score (axis 1 of PCA), abundance outside Paris, body size and feeding regime as fixed effects, and the random effects listed previously. Abundance in the Ile-de-France region outside Paris was included in the model because the probability of breeding of a species in any locality most likely increases with its overall abundance in the region and has to be statistically controlled for.

Second, we tested for an association between density and colouration, and whether this association would depend on the zone (inside versus outside Paris). For this, we had to distinguish between species breeding both inside and outside Paris and those which do not breed inside Paris. For species breeding both inside and outside Paris, we fitted linear mixed-effects model with log-transformed mean density as dependent variable, melanin colouration score, zone (inside versus outside Paris), their interaction, body size and feeding



regime as fixed effects, and the random effects listed previously, with Species additionally nested within Genus (to account for non-independency of data for a given species between both zones). We further fitted 2 separate models similar to the latter (without zone and zone  $\times$  melanin interaction), respectively with log-transformed density 1) inside and 2) outside Paris.

For species not breeding inside Paris (but only outside Paris), we finally tested for a relation between log-transformed density outside Paris and colouration, using the same type of model as the latter described.

Complete models were progressively simplified to final models by removing non-significant terms. Statistical analyses were performed using R (ver. 4.1) and RStudio (ver. 1.4.1717), with packages rptR (for repeatability; Stoffel et al. 2017), MASS (glmmPQL, handling quasi-distributions in mixed effects models on non-integer values), car (which function Anova allows extracting  $\chi^2$  associated with global effects), dplyr, ggplot (Wickham 2016) and ggeffects (for predicted values in the figures; Lüdtke 2018). Presentations of figures for binomial models follow Smart et al. (2004), incorporating frequency histograms to the classic probability plot.

## Results

### Number of bird species inside and outside Paris

Among the 151 bird species breeding in the whole Ile-de-France region, 60 (40%) were also recorded as breeding within the city of Paris, while the remaining 91 species (60%) were not recorded as breeding there, thus breeding outside the city only.

### Reliability of scoring methods

Scoring methods appeared highly repeatable among observers (binary score: point estimate  $R=0.84$ , standard error  $SE=0.14$ , confidence interval  $CI=[0.50, 0.99]$ ,  $p=6 \times 10^{-11}$ ; first continuous score:  $R=0.82$ ,  $SE=0.07$ ,  $CI=[0.64, 0.91]$ ,  $p=1 \times 10^{-12}$ ; second continuous score:  $R=0.88$ ,  $SE=0.05$ ,  $CI=[0.74, 0.95]$ ,  $p=1 \times 10^{-08}$ ). In addition, the three melanin colouration scoring methods used gave highly correlated estimations: the simple binary scoring was correlated to both the simple ( $\chi^2_1=54.55$ ;  $p=2 \times 10^{-13}$ ) and the complex ( $\chi^2_1=21.51$ ;  $p=4 \times 10^{-06}$ ) continuous scoring methods, as were both continuous methods ( $\chi^2_1=60.94$ ;  $p=6 \times 10^{-15}$ ). Along with the successful use of such methods in previous studies (Yezerinac and Weatherhead 1995, Biard et al. 2009, Leveau et al. 2019) and the high repeatability of the second continuous scoring method found previously ( $R > 0.87$ ; Biard et al. 2009), we were thus confident in their reliability given our biological hypothesis.

The coordinate of each bird species along the first axis of the principal components analysis (representing 99.54% of the total variance) was extracted and used as melanin score (higher values of indicated darker melanin plumage colourations), along with the mean of scores.

### Factors associated with breeding inside Paris

As predicted, the distribution of melanin score was higher among species breeding both inside and outside Paris (mean = 2.74,  $SE=1.68$ ) than species breeding outside Paris only (mean = -1.81,  $SE=1.11$ ;  $D=0.27$ ,  $p=0.007$ ; see distributions in Fig. 1).

The probability of breeding inside Paris was not influenced by feeding regime of bird species ( $\chi^2_5=2.79$ ,  $p=0.73$ ) but increased significantly with melanin colouration score as predicted ( $\chi^2_1=4.89$ ,  $p=0.027$ ; Fig. 1), and, not surprisingly, with abundance outside Paris ( $\chi^2_1=15.61$ ,  $p=8 \times 10^{-05}$ ; Supporting information); it significantly decreased with increasing body size ( $\chi^2_1=4.83$ ,  $p=0.028$ ; Supporting information).

For species breeding both inside and outside Paris, density was neither significantly associated with feeding regime ( $\chi^2_5=8.73$ ,  $p=0.12$ ), nor with body size ( $\chi^2_1=0.99$ ,  $p=0.32$ ), but with the colouration  $\times$  zone interaction as predicted ( $\chi^2_1=9.05$ ,  $p=0.003$ ). More specifically, their density increased with colouration intensity inside Paris (Fig. 2Aa) whether controlling ( $\chi^2_1=13.12$ ,  $p=0.0003$ ) or not ( $\chi^2_1=7.44$ ,  $p=0.006$ ) for abundance outside Paris, which not surprisingly also appeared significant ( $\chi^2_1=33.20$ ,  $p=8 \times 10^{-09}$ ). Outside Paris, density of these species was not significantly associated with colouration intensity ( $\chi^2_1=2.28$ ,  $p=0.13$ ; Fig. 2Ab).

For species not breeding inside Paris, density was not associated with body size ( $\chi^2_1=0.64$ ,  $p=0.42$ ), but with feeding regime ( $\chi^2_5=40.84$ ,  $p=1e-7$ ; Supporting information) and decreased with increasing colouration score ( $\chi^2_1=4.40$ ,  $p=0.036$ ; Fig. 2B).

## Discussion

We found several lines of evidence indicating that urbanization not only appears to be associated with a shift in species composition towards melanic bird species, but even to shape the relation between density and melanin-based colouration. First, the distribution of melanin colouration intensity was higher inside than outside the city. Second, both the probability of breeding inside the city and the density within the city increased with melanic colouration intensity of bird species. Importantly, these associations were not confounded with abundance outside Paris, which was statistically controlled for and, not surprisingly, appeared significant. Third, for species breeding both inside and outside Paris, the positive association between density and melanic colouration was only observed inside and not outside the city, hence did not simply reflect a general relation between density and colouration intensity. Fourth, the density of species not breeding in Paris decreased with increasing melanic colouration.

Cities have previously been shown to act as environmental filters in various taxa. In birds, urban communities are characterized by lower species richness, with higher densities of species, exhibiting a series of morphological, behavioural and physiological characteristics (Bonier et al. 2007, Evans et al.

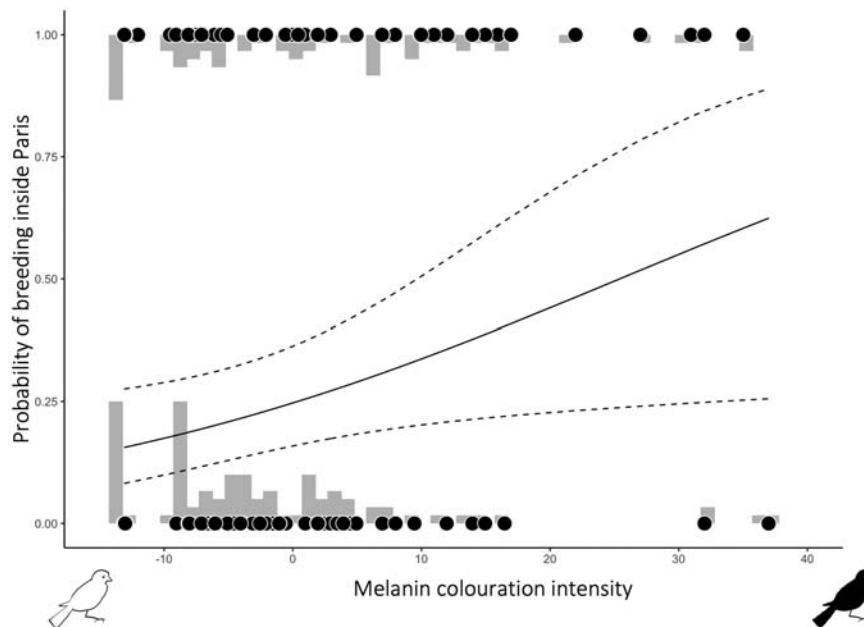


Figure 1. Probability of breeding inside Paris plotted against melanin-based colouration intensity (first axis of principal correspondence analysis) of the 151 bird species breeding in Île-de-France region. Black circles with values 0 (not breeding inside Paris,  $n = 91$ ) or 1 (breeding inside Paris,  $n = 60$ ) indicate the observed data. The continuous line represents the predicted values from the final model including other fixed and random effects; dashed lines correspond to lower and higher range of 95% confidence interval. Grey bars represent melanin score distribution among species breeding (top) or not (bottom) inside Paris.

2011, Sol et al. 2014, Marzluff 2017, Ducatez et al. 2018, Isaksson 2018, Leveau 2019). Our results confirm that body size is not neutral with regards to the ability of bird species to breed in the city (Supporting information). In addition, the probability of breeding in the city increased with abundance outside Paris (Supporting information); this (rather trivial) observation is obviously expected because urban success is most likely influenced by the source pool of available species, and indicates that this variable had to be statistically controlled for, which was here. Absence of a species in any given locality (e.g. in a city) may indicate that it has had few opportunities to colonize it (Clergeau et al. 2001, Sol et al. 2014) for example because it lives in remote regions too far away, or because its abundance is too low to generate propagules (Ducatez et al. 2018). Here, we lessened the effect of such demographic constraints by both considering a restricted spatial scale (limiting the possibility that a given bird species was simply too far to colonize the city) and controlling for overall species abundance in the region (hence its rarity).

A much more original result of our study is the covariation between urbanization and bird melanin colouration observed, even when statistically controlling for the previous covariables. A recent review provided strong evidence that urbanization is related to intra- and interspecific changes in animal colours in several taxa (birds, insects, amphibians, reptiles), however pointing out important taxonomic and geographical biases (Leveau 2021). Similarly to Leveau (2019, 2021), our results show a covariation between melanin colouration and urbanization, though the precise relations somewhat differ between studies. Slight differences might not be surprising, as

many additional factors influence bird communities (e.g. rate and time since urbanization, Aronson et al. 2014; local and global, abiotic and biotic environmental conditions, Martin and Bonier 2018). Overall, such similar results on covariation between urbanization and melanin-based colouration (and marginally body size) found in very distant geographic regions and among very different local avian communities strongly suggest that this trend may be general in birds and in other taxa.

Even more interestingly, our work provides the first evidence to the best of our knowledge that urbanization shapes the relation between melanic colouration and density. The density of bird species breeding both inside and outside Paris increased with melanin colouration intensity inside Paris, but not outside Paris. Importantly, this relation was found even when controlling for the (obviously highly significant) abundance outside Paris. In addition, the density of bird species not breeding in the city decreased with increasing colouration intensity. The relation between density and melanic colouration thus depends on urbanization-associated environmental factors: melanic species do not thrive everywhere. Overall, these results first confirm our prediction that pronounced melanic colouration is advantageous in urbanized areas. Second, they suggest that, at least in temperate regions such as the one studied here, the balance between advantages and costs of intense melanic colouration may depend on habitat: beneficial in urbanized areas (since the probability to breed and the density inside the city increase with melanic colouration), but detrimental in less urbanized ones (since outside the city the density of species not breeding in the city decreased

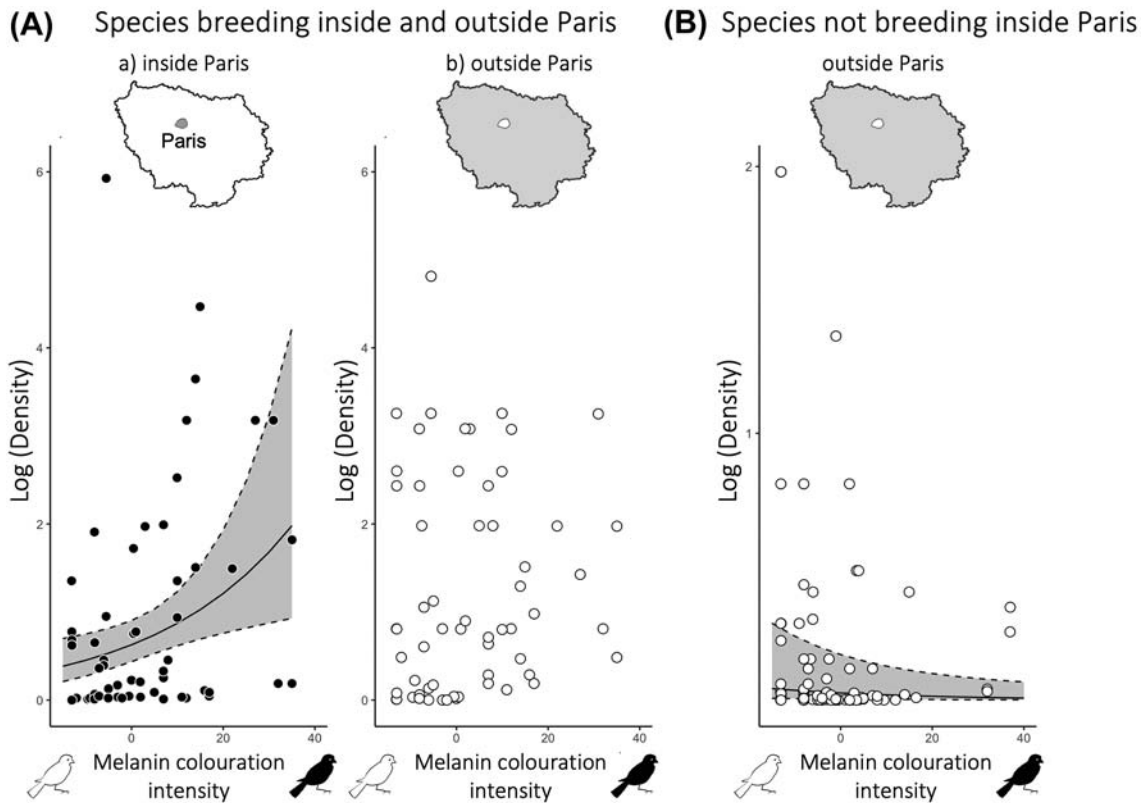


Figure 2. Mean density plotted against melanin colouration intensity for the 60 bird species breeding both inside and outside Paris (A) and the 91 bird species not breeding inside Paris (B), measured either inside (black circles in Aa) and outside Paris (white circles in A-b and B). Circles represent raw data; the lines correspond to the predicted values from the models including other potential fixed and random effects. Note that densities in A and B are on different scales.

with increasing melanin colouration). This hypothesized cost of pronounced melanic coloration in less urbanized areas may however not be a general trend, as the balance between costs and benefits is likely influenced by local environmental factors that may favour dark coloration even outside cities (abiotic and biotic environmental conditions (Martin and Bonier 2018) such as temperature, concentration of metals, population sizes...). In cold regions for example, pronounced melanic colorations may be advantageous because of the thermal advantage they confer.

Identifying both the precise environmental drivers and the exact melanin-associated trait(s) involved in this cost-benefit balance remains quite elusive in our correlative approach (as for intraspecific studies; Isaksson 2018). Melanin-coloration may either be directly involved in this balance per se, or indirectly due to its association with any of the numerous associated traits influenced by environmental driver(s). Indeed, melanin synthesis and coloration intensity are associated with a considerable series of phenotypic characteristics, either positively (skin pigmentation, resistance to abrasion (Bonser 1995), metal chelation (Hong and Simon 2007), anti-inflammatory activity, HPA stress response and steroidogenesis, energy expenditure, cardiovascular and anti-inflammatory activity, resistance to stressors including oxidative and physiological stress, sexual activity, aggressiveness, natriuresis,

antipyretic and antiapoptotic activity, exocrine gland activity) or negatively (nociception, food intake, grooming and autoimmune response; reviewed by Ducrest et al. 2008 and McNamara et al. 2021). Melanin-based coloration can thus interestingly be used as an integrative phenotypic marker associated with many other traits.

At the intraspecific level, polymorphic species (insects, birds, reptiles) tend to be more melanic in urban areas, possibly due to camouflage, to resistance to parasitism (Jacquin et al. 2013), to stress response (Corbel et al. 2016), to metal detoxification (Chatelain et al. 2014, 2016) and perhaps to resistance to feather-degrading bacteria (Gunderson 2008, Azcárate-García et al. 2020) and parasites, more abundant in the cities (Giraudeau et al. 2014, 2016). At the interspecific level, some of the factors previously proposed for the increasing proportion of melanic individuals along urbanization within species may also be involved in the urban-associated costs–benefits balance of melanic coloration among species. Since melanin production per se is supposed to bear no cost in vertebrates (McNamara et al. 2021; for other taxa, Stoehr 2006), other disadvantages must be responsible for costly melanin-based coloration in less urbanized habitats. In Argentinian cities, camouflage has been proposed as a main factor responsible for the predominance of species with grey plumage and uniform plumage lightness, potentially in

response to predators and pedestrians (Leveau 2019, Leveau and Ibáñez 2022). In Paris, predators likely do not represent the main factor in environmental filtering because they are scarce (mainly restricted to some peregrin falcons *Falco peregrinus*, Eurasian sparrowhawk *Accipiter nisus*, common kestrel *Falco tinnunculus*, European herring gull *Larus argentatus*, carrion crow *Corvus corone*, as well as cats and dogs). The urbanization-associated balance between costs and benefits of melanin-based colouration observed in our study thus likely result from other factors. For instance, melanin-driven metal sequestration in feathers might allow melanic species to thrive in cities dominated by high concentrations of toxic metals from numerous sources (Hill 2020), as observed within species (Chatelain et al. 2014, 2016); on the opposite, high concentrations of melanin in inert body parts such as feathers could be detrimental in areas where the majority of metals rare beneficial essential elements, as these would be sequestered outside the bloodstream and the organs, thus penalizing them with metal deficiency in less urbanized environments. The production itself of melanin requires metals, which may be less present in non-urban versus urban areas. Melanic species with higher stress response may better cope with high urban disturbances (Corbel et al. 2016) but pay the associated oxidative stress in rural areas. Melanin-linked aggressive behaviour (Ducrest et al. 2008) may provide melanic species with behavioural dominance causing higher abundances in urban habitats (Martin and Bonier 2018), but be energetically costly in less competitive habitats. Predictable abundant food resources in cities may allow melanic species to sustain energetic costs associated with high immunity (Côte et al. 2018), whereas opposite environmental conditions may be favourable to paler species. Most probably, the habitat-specific costs–benefits balance linked with melanin colouration may be multifactorial: melanin colouration and associated traits altogether may cause high and low relative densities of melanic species in urban and less urbanized areas respectively, due to various abiotic and biotic drivers. As a consequence, melanic species would reach higher densities in the cities and less melanic would do so in rural areas, resulting in the habitat-specific relations observed. Contrary to species absent from Paris, species breeding in Paris did not exhibit a decreasing density outside Paris with increasing melanin-based colouration intensity, probably because they may still breed in moderately urbanised areas in the Parisian agglomeration (representing a surface of 2853.5 km<sup>2</sup>) outside the city of Paris itself. Indeed, urban bird species tend to also live in other artificial habitats outside the cities (Ducatez et al. 2018). As for intraspecific studies (Isaksson 2018), identifying the precise driver(s) and the particular trait(s) involved in this balance requires further investigation. Importantly, that melanin-rich colouration is detrimental outside cities is probably not generalizable worldwide, as local conditions likely influence the cost-balance benefits associated with melanin-based coloration.

The shift in community composition observed here does not preclude additional evolutionary or plastic responses within member species (Brans et al. 2020), which could be

further analyzed by specifically measuring potential intra-specific differences in melanic colouration intensity between urban and rural populations. However, our results suggest that if adaptive evolution does occur on this trait, it may be too weak to buffer shifts in community composition along urbanization gradients (Brans et al. 2020). This is somewhat not surprising, given that adaptive evolution on a trait requires phenotypic variation while most of the species studied here are not polymorphic with regards to melanin-based colouration.

We did observe interesting associations in line with our predictions despite the simple approaches used. We used reliable but simple scoring methods (previously successfully used: Yezzerinac and Weatherhead 1995, Biard et al. 2009, Leveau et al. 2019). We simply distinguished Paris intramuros versus the rest of the region, though urbanization obviously does not abruptly stop at the administrative boundaries, which birds likely can cross. Species loss seems to happen especially at the urban–suburban interface (Batáry et al. 2018), which in the case of Paris would be far away from the administrative boundary. The region itself is one of the most urbanized regions in Europe, and the precise range of urbanization obviously influences its influence on biodiversity (Batáry et al. 2018, Leveau 2021). Consequently, our study focuses on a rather limited and elevated range of urbanization gradient, and most probably underestimates the overall relation between urbanization and body colour in the whole region. In other regions of the globe, other environmental factors may modulate the relations observed here. We only included breeding species to limit the importance of few erratic individuals, but breeding attempts may be poorly successful or unsuccessful: cities may act as sinks (without any particular preference towards cities) or even ecological traps (with preference towards cities due to apparent favorable conditions; Isaksson 2018; but see Zuñiga-Palacios et al. 2021). Further work is needed to gain insight into the relations found, including a broader range of both urbanization rates and of contrasted environmental conditions worldwide, a more precise evaluation of melanic colouration intensity and of local habitats, more precise data on population sizes and on breeding success, and other important bird traits (such as nesting behavior and migration).

Global change is currently considered as responsible for dramatic biodiversity erosion. Growing urbanization constitutes one of its main factors and urges to dig more deeply into how contrasted urbanized habitats may differentially affect species and ecological communities (Leveau 2021) by shaping the relations between interspecific variation in traits and species densities worldwide, and investigating the consequences of these environments remains crucial.

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## Author contributions

**Neyla Turak** and **Alice Monnier-Corbel** contributed equally to this publication. **Neyla Turak**: Data curation (equal). **Alice Monnier-Corbel**: Data curation (equal). **Mélanie Gouret**: Data curation (equal). **Adrien Frantz**: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Supervision (lead); Validation (lead); Writing – original draft (lead).

## Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.k6djh9w9b>> (Turak et al. 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

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